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A review of pathogens in selected Baltic Sea indicator species

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ABSTRACT

Here we review the state-of-the-art of pathogens in select marine and terrestrial key species of the Baltic Sea, i.e. ringed seal (*Pusa hispida*), harbour seal (*Phoca vitulina*), grey seal (*Halichoerus grypus*), harbour porpoise (*Phocoena phocoena*), common eider (*Somateria mollissima*), pink-footed goose (*Anser brachyrhynchus*) and white-tailed eagle (*Haliaeetus albicilla*). This review is the first to merge and present available information and baseline data for the FP7 BONUS BaltHealth project: *Baltic Sea multilevel health impacts on key species of anthropogenic hazardous substances*. Understanding the spread, prevalence and effects of wildlife pathogens is important for the understanding of animal and ecosystem health, ecosystem function and services, as well as human exposure to zoonotic diseases. This review summarises the occurrence of parasites, viruses and bacteria over the past six decades, including severe outbreaks of Phocine Distemper Virus (PDV), the seroprevalence of Influenza A and the recent increase in seal parasites. We show that Baltic high trophic key species are exposed to multiple bacterial, viral and parasitic diseases. Parasites, such as *C. semerme* and *P. truncatum* present in the colon and liver Baltic grey seals, respectively, and anisakid nematodes require particular monitoring due to their effects on animal health. In addition, distribution of existing viral and bacterial pathogens, along with the emergence and spread of new pathogens, need to be monitored in order to assess the health status of key Baltic species. Relevant bacteria are *Streptococcus* spp., *Brucella* spp., *Erysipelothrix rhusiopathiae*, *Mycoplasma* spp. and *Leptospira interrogans*; relevant viruses are influenza virus, distemper virus, pox virus and herpes virus. This is of special importance as some of the occurring pathogens are zoonotic and thus also pose a potential risk for human health. Marine mammal handlers, as well as civilians that by chance encounter marine mammals, need to be aware of this risk. It is therefore important to continue the monitoring of diseases affecting key Baltic species in order to assess their relationship to population dynamics and their potential threat to humans. These infectious agents are valuable indicators of host ecology and can act as bioindicators of distribution, migration, diet and behaviour of marine mammals and birds, as well as of climate change and changes in food web dynamics. In addition, infectious diseases are linked to pollutant exposure, overexploitation, immune suppression and subsequent inflammatory disease. Ultimately, these diseases affect the health of the entire ecosystem and, consequently, ecosystem function and services. As global warming is continuously increasing, the impact of global change on infectious disease patterns is important to monitor in Baltic key species in the future.

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Fig. 1. An overview of the Baltic Sea area from which marine mammal and bird species are reported. This area shows the HELCOM area the research project BaltHealth.

1. Introduction

The Baltic Sea is a semi-enclosed brackish water system in northern Europe bordered by nine countries and an estimated 85 million people whose livelihood is directly or indirectly linked to the ecosystem services provided by the Baltic Sea (Fig. 1) (HELCOM, 2018). The geophysical features of the Baltic Sea are characterised by partial isolation, large salinity gradients and temporal fluctuations in e.g. bottom oxygen levels. These features have contributed to a unique composition of marine fauna, including a wide variety of viral, bacterial and parasitic pathogens either localised to specific regions or species, or spread widely in the ecosystem (Johannesson and André, 2006). Pathogens such as Phocine Distemper Virus (PDV) and Influenza A have repeatedly caused mass mortalities among key species of the Baltic Sea ecosystem (Härkönen et al., 2006; Zohari et al., 2014), and it seems the number of diseases registered in the Baltic Sea is higher than in other marine systems (Siebert et al., 2009). This includes an increased parasitic burden in fish and marine mammals, as well as the Baltic Seal Disease Complex (BSDC) (Bergman, 2007). BSDC includes multiple chronic organ lesions in female reproductive organs (uterine stenosis and occlusions), intestines (colonic ulcers) and adrenals (cortical hyperplasia), as well as severe lesions in the skeleton, integument and kidneys (Bergman, 2007). It has been discussed that this was caused by high levels of pollutants such as the organochlorines polychlorinated biphenyls (PCB) and dichlorodiphenyltrichloroethane (DDT) (Bergman, 2007). A detailed knowledge of pathogens and animal health is crucial for understanding their effect on marine ecosystem function and diversity, including detrimental or beneficial effects on ecosystem services, pathogen reservoirs and zoonotic potential, and the putative role of overexploitation, pollution, eutrophication, noise and climate change on the likelihood of pathogen transmission, susceptibility and/or

mortality. Here, we describe pathogens found in select marine and terrestrial Baltic species designated as indicators of ecosystem health by HELCOM: the ringed seal (*Pusa hispida*), harbour seal (*Phoca vitulina*), grey seal (*Halichoerus grypus*), harbour porpoise (*Phocoena phocoena*), white-tailed eagle (*Haliaeetus albicilla*), common eider (*Somateria mollissima*) and pink-footed goose (*Anser brachyrhynchus*). The aim was to understand and mitigate the cumulative effects of pathogens and anthropogenic and natural stressors on marine ecosystem health and function. Although focusing on the Baltic Sea, we anticipate that our review will aid in understanding the effects of pathogens in other less studied, albeit equally exposed, marine ecosystems.

2. Literature survey

The review builds on the authors' own experience with pathogens identified in the six species appointed by HELCOM as health indicators in the Baltic Sea ecosystem: the white-tailed eagle, common eider, pink-footed goose, grey seal, harbour seal, ringed seal and harbour porpoise. Furthermore, we used ScienceDirect, PubMed, Google, Google Scholar, ISI Web of Knowledge/Web of Science and Springer Link to locate peer-reviewed scientific articles and reports. We used the following key words (either alone or in combination): avian, bird, fish, cod, marine mammal, seal, harbour seal, grey seal, ringed seal, harbour porpoise, eider, white-tailed eagle, pink-footed geese, infectious diseases, parasite, virus and bacteria, including species scientific names. The number of final hits depended highly on species, additional key words and search engine ranging 10 to greater than 100,000. Hereafter, the searches was adjusted to the scope, species and geographical patterns of the review and the final hits was then < 500 from which the most relevant literature was selected. We also used educational and scientific textbooks, along with the references cited in these books and within the

Table 1
Overview of infectious agents reported in the literature for selected Baltic Sea indicator species. For bacteria, only known pathogens are shown. Blank: data not available.

	Lung/ear parasite	Heart parasite	Liver parasite	Gastric parasite	Intestinal parasite	Phocine Distemper Virus	Porpoise morbillivirus	Influenza A Virus	<i>Erysipelothrix rhusiopathiae</i>	<i>Streptococcus</i> sp.	<i>Staphylococcus</i> sp.	<i>Brucella</i> sp.	<i>Escherichia coli</i>	<i>Pseudomonas</i> sp.
Ringed seals		×		×	×	×				×	×			×
Grey seals			×	×	×	×		×		×	×	×	×	
Harbour seals	×			×	×				×	×	×	×		
Harbour porpoises	×		×	×	×		×			×	×	×		×
Common eiders														
White-tailed eagles					×			×						

chosen scientific articles. Although we attempted a systematic literature search, we acknowledge that this, e.g. due to language and/or availability constraints such as some Russian reports, is not an exhaustive representation of all information found in the scientific literature worldwide. The overview of infectious agents reported in the literature for selected Baltic Sea indicator species is summarized in Table 1.

3. Parasites

The Baltic Sea is a special biotope for parasites and hosts due to factors like salinity, pollution and anthropogenic activities affecting the animals' health, life cycles and population structures (Garbus et al., 2018; Morell et al., 2017). Parasites are valuable markers of animal and ecosystem health and reflect food web dynamics by acting as indicators for diet and trophic interactions, as well as inform about migrations and habitat use (Marcogliese, 2002). In addition, some parasites (ectoparasites like lice, mites and crustaceans) rely on direct transmission and can help us to understand the behaviour, distribution and population (Reckendorf et al., 2019). Thus, the study of these organisms is relevant for monitoring the environmental status and fauna of the ecosystem in order to assess and handle future changes and impacts, e.g. for adequate species conservation.

3.1. Marine mammal parasites

Grey seals, harbour seals, ringed seals and harbour porpoises are top predators in the Baltic Sea and act as final hosts for various ecto- and endoparasites. These parasites include nematodes, trematodes and acanthocephalans infecting the lungs and gastrointestinal tract (stomach, liver, pancreas, intestines), in addition to lice, mites, crustaceans and protozoan (Lehnert et al., 2007; Siebert et al., 2001).

A large fraction of these parasites are transmitted trophically by prey fish species, which are their paratenic or obligatory intermediate hosts (Zander and Reimer, 2002). Some parasites, however, rely on direct transmission, and in multiple species the life cycles are still not elucidated (e.g. trematodes) or not fully understood (e.g. lungworms).

3.1.1. Lung and gastrointestinal nematodes

The most abundant and pathogenic parasites for marine mammals are lung and gastrointestinal nematodes (Measures, 2001; Ulrich et al., 2016). There are two lungworm species infecting seals in northern European waters, *Otostrongylus circumlitus* (Crenosomatidae) and *Parafilaroides gymnuris* (Filaroididae; Metastrongyloidea) (Lehnert et al., 2007; Siebert et al., 2007) (Fig. 2), whereas harbour porpoises are infected by three lungworm species, *Pseudalius inflexus*, *Torynurus*



Fig. 2. Severe lung nematode infection (arrows) and associated bronchopneumonia in a harbour seal.

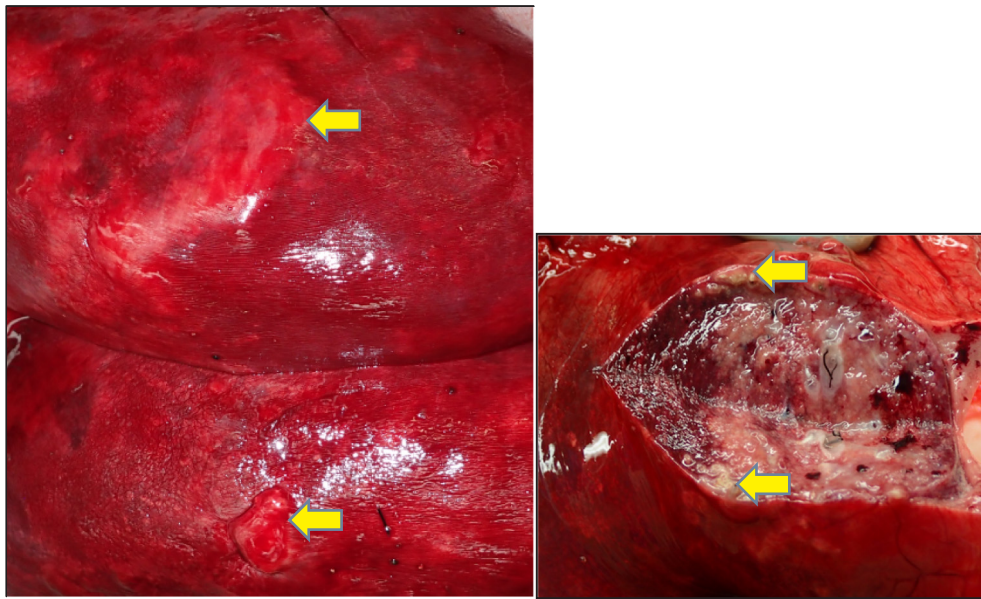


Fig. 3. Granulomatous bronchopneumonia (arrows) caused by lung nematodes in a harbour porpoise.

convolutus and *Halocercus invaginatus* (Pseudaliidae, Metastrongyloidea) (Lehnert et al., 2005). Affected seals often present secondary, opportunistic bacterial infections with a suppurative, suppurative-necrotising and/or pyogranulomatous/granulomatous bronchopneumonia. In harbour porpoises, parasites often cause the development of histiocytic and eosinophilic broncho-interstitial pneumonia, chronic thrombosis and vasculitis, catarrhal-suppurative, suppurative-necrotising pneumonia or granulomatous pneumonia (Siebert et al., 2001; Lehnert et al., 2007) (Fig. 3). In harbour seals, lungworm infections are highly age-related, often causing mortality in pups-of-the-year while adults generally present milder infections, if any. It is assumed that they acquire protective immunity after surviving initial infections (Ulrich et al., 2016). In porpoises, on the contrary, lungworms seem to accumulate with age, as older animals tend to have more lungworms than to young animals (Lehnert et al., 2005). Another pseudaliid nematode (*Stenurus minor*) has established an ecological niche in the nasal sinuses, eustachian tubes and aural *peri*-bullar cavity in harbour porpoises, often occurring in large numbers (Lehnert et al., 2005; Siebert et al., 2001). Furthermore, these nematodes may be able to impair hearing when migrating to the inner ear and damaging the structures located there (Morell et al., 2017). Whether or not this nematode is a factor responsible for bycatch or strandings because of acoustic impairment due to inflammatory alterations and sound blockade is uncertain (Faulkner et al., 1998; Morell et al., 2017), but the often severe infections may induce stress and pain (Kijewska et al., 2003).

In seals, the anisakid nematodes *Pseudoterranova decipiens* and *Contracaecum osculatum* are regularly found in the stomach (Fig. 4) and can be associated with diffuse catarrhal and lymphocytic gastritis, as well as with chronic ulcerative gastritis (Lehnert et al., 2007) (Fig. 5). Those infections are mostly mild and associated lesions are seldom severe. Harbour porpoises are infected by *Anisakis simplex*, sometimes in association with chronic ulcerative gastritis (Lehnert et al., 2005; Siebert et al., 2001) (Fig. 6). Third stage infectious larval anisakid nematodes are harboured by multiple fish intermediate host species (Kuhn et al., 2013) and cause the zoonotic disease anisakiasis when live larvae from undercooked fish are accidentally ingested by humans (Baird et al., 2014). Anisakid larvae have shown some resistancy toward smoking, salting and marinating as well as toward freezing (Gardiner, 1990; Sánchez-Alonso et al., 2018). They may cause gastric symptoms like nausea, vomiting, acute pain or potential allergic reactions in humans (Shamsi, 2019). A few human cases of anisakiasis were identified



Fig. 4. Severe gastric nematode infection (arrows) in a grey seal.

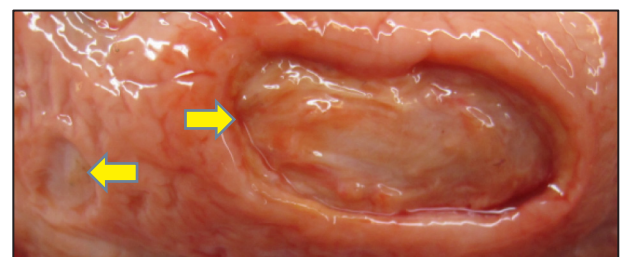
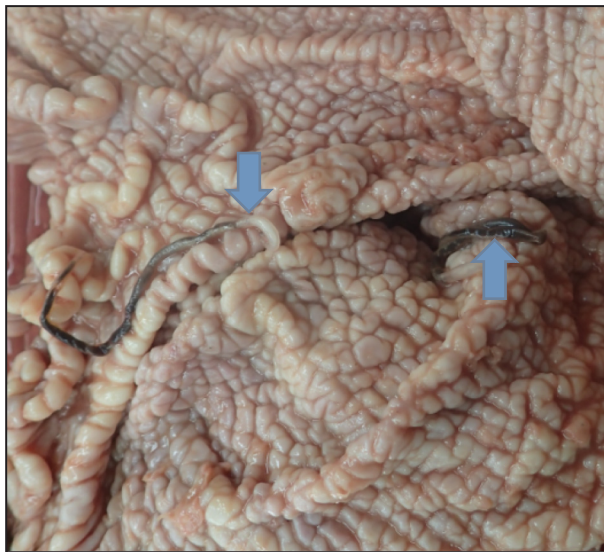


Fig. 5. Severe gastric ulcers (arrows) caused by gastric nematodes in a grey seal.

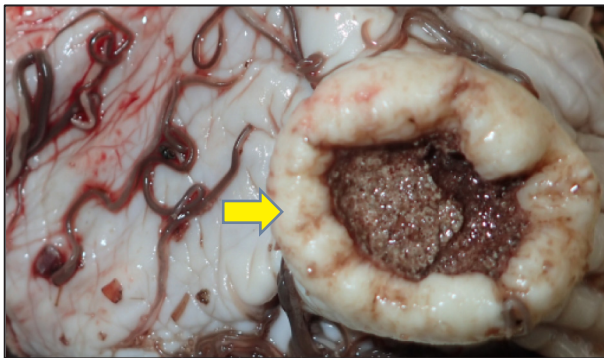
as resulting from eating under-cooked fish, like herring, caught in the Baltic Sea during the 1960s and 1980s (Knöfler and Lorenz, 1982; Schaum and Müller, 1967).

3.1.2. Gastric and liver trematodes

The gastric trematode *Pholeter gastrophilus* is present in the second and fourth stomach compartments of harbour porpoises and other cetaceans, and is often associated with granulomatous gastritis (Lehnert et al., 2005; Siebert et al., 2001). *Pseudamphistomum truncatum* is a newly emerging zoonotic liver fluke in Baltic grey seals, with the roach (*Rutilus rutilus*) as a paratenic host, associated with chronic inflammation, fibrosis and liver failure (Neimanis et al., 2016) (Fig. 7). Harbour



a



b

Fig. 6. *Anisakis simplex* infection in a harbour porpoise and associated gastric ulcer (first stomach compartment, arrows).

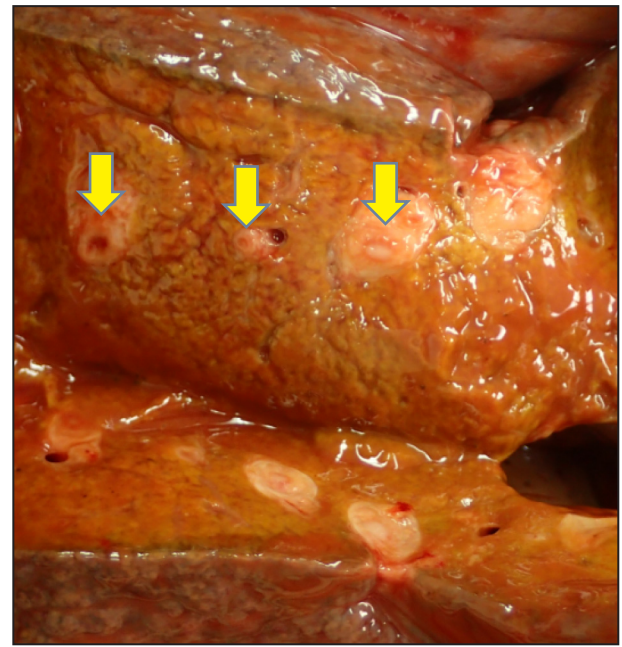


Fig. 8. Severe bile duct hyperplasia (arrows) caused by *Campula oblonga* in a harbour porpoise.

porpoises are infected by the fluke *Campula oblonga* in the liver and pancreas, which often induces cholangitis, pericholangitis, portal and periportal fibrosis (Fig. 8), biliary hyperplasia and periductular fibrosis, inflammation of the pancreatic ducts and pancreatitis (Lehnert et al., 2005; Siebert et al., 2001).

3.1.3. Acanthocephala

Acanthocephalans of the genus *Corynosoma* are very common in the small and large intestines of seals (Waendok et al., 2018) and play an important role in colonic lesions of the BSDC, especially *Corynosoma semerme* (Bergman, 1999, 2007).

Three acanthocephalan species from the genus *Corynosoma* occur in the Baltic Sea, *Corynosoma strumosum*, *Corynosoma magdalenae* and *C. semerme*, with grey seals, ringed seals and harbour seals as final hosts

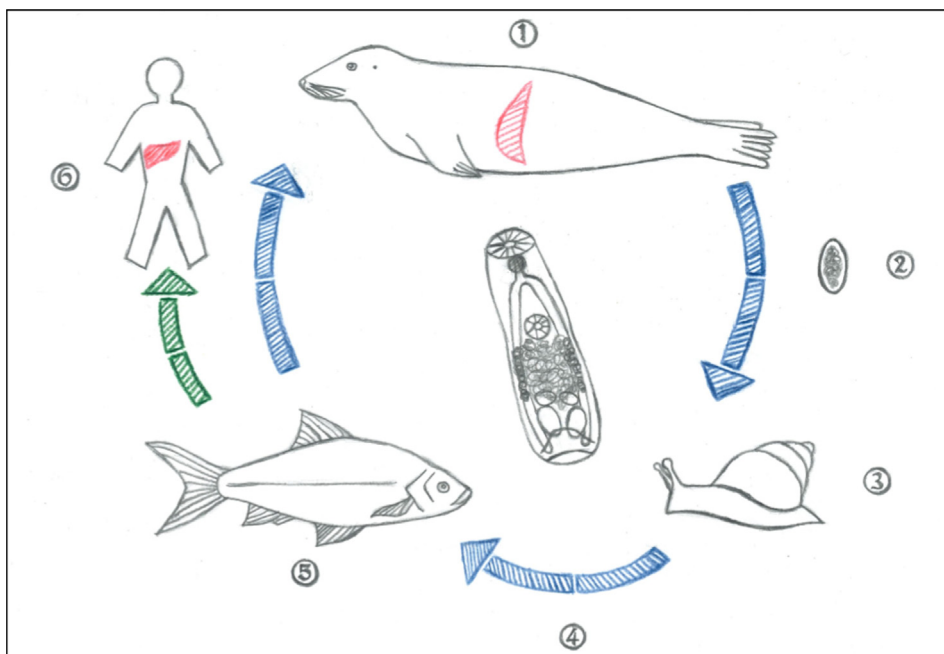


Fig. 7. Life cycle of *Pseudamphistomum truncatum*. 1: grey seal final host, infected liver (red); 2: eggs containing miracidium shed with faeces; 3: first intermediate host snail ingests trematode eggs, development of trematode larval stages: miracidium -> sporocyst -> redia -> cercaria in snail; 4: cercariae released from snail; 5: cercariae encyst as metacercariae in second intermediate host (cyprinid fish, e.g. roach) after fish ingests snail; 1/6: final host grey seal (1) or accidental host human (6), ingest fish with metacercariae, metacercariae develop to adults in bile ducts.

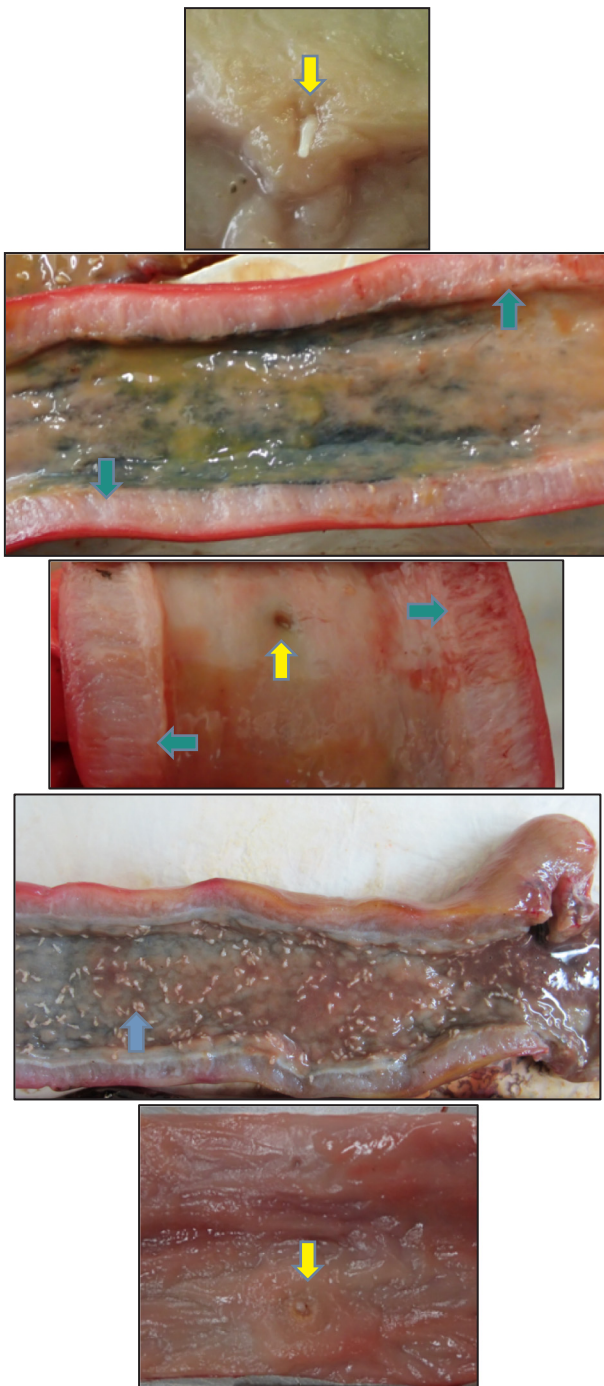


Fig. 9. Severe *Corynosoma semerme* infection in the colon (blue arrow) and associated lesions: colonic ulcers (yellow arrows) and *tunica muscularis* hypertrophy (green arrows) in a grey seal.

(Nickol et al., 2002; Sinisalo and Valtonen, 2003; Valtonen et al., 2004). *C. strumosum* and *C. magdaleni* infect the seals' small intestine, whereas *C. semerme* infects the caecum and colon (Nickol et al., 2002). The small intestinal *Corynosoma* spp. can cause granulomatous eosinophilic mural enteritis accompanied by lympho-plasmacytic and lympho-histiocytic enteritis (Lakemeyer et al., in press) (Fig. 9). Grey seals infected with *C. semerme* displayed a chronic eosinophilic or lympho-plasmacytic or erosive to ulcerative colitis, as well as a colonic *tunica muscularis* hypertrophy (Lakemeyer et al., in press). Intriguingly, the prevalence of *Corynosoma* spp. appears to have changed during the last 30 years. In ringed seals investigated from 1988 to 1999 by Valtonen et al. (2004),

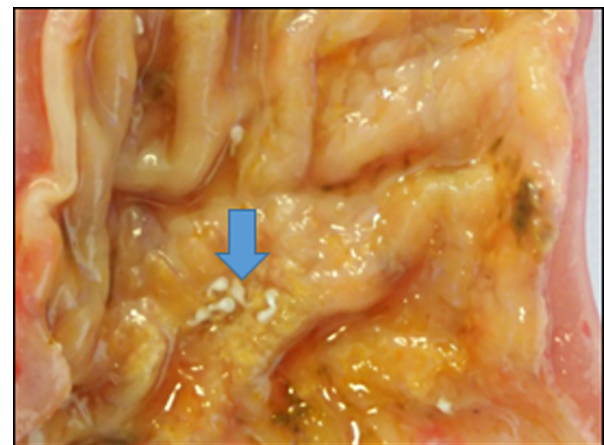


Fig. 10. *Corynosoma semerme* infection (arrow) in a ringed seal colon.

the prevalence of *C. strumosum* decreased from 80% in 1988 to 71% in 1999. In a study by Nickol et al. (2002) investigating grey seals in 1986–1987, the prevalence of *C. strumosum* decreased from 85% to 31%. A potential cause for the decline of *C. strumosum* since the 1990 s is the disappearance of its most important paratenic host, the shorthorn sculpin (*Myoxocephalus scorpius*), caused by a reduction in the salinity of the Baltic Sea (Nickol et al., 2002; Sinisalo and Valtonen, 2003; Valtonen et al., 2004). The prevalence of *C. magdaleni* increased from 69% to 92% in grey seals in the period 1986–1987 (Nickol et al. 2002). *C. semerme* is very abundant in Baltic seals with 100% prevalence in ringed (Fig. 10) and grey seals over the past 30 years (Nickol et al., 2002; Valtonen et al., 2004), as well as more than 80% prevalence in its main paratenic host, the fourhorn sculpin (*Myoxocephalus quadricornis*), in samples collected 1977–1982 and 1996–1997 (Sinisalo and Valtonen, 2003). The fourhorn sculpin is better adapted to brackish water than its congener, the shorthorn sculpin, thereby supporting the life cycle and occurrence of *C. semerme* in the Baltic Sea (Sinisalo and Valtonen, 2003; Valtonen and Helle, 1988) (Fig. 11), and thus putatively becoming a major parasite in Baltic grey seals (Bäcklin et al., 2013, 2011; Bergman, 2007, 1999; Lakemeyer et al., in press).

3.1.4. Heart nematodes and seal lice

The filarial nematode *Acanthocheilonema spirocauda* parasites the heart chambers of harbour seals (Geraci et al., 1981; Lehnert et al., 2007). The life cycle of the heartworm is not fully understood, but available data indicate that this parasite may utilise the seal louse *Echinophthirius horridus* as its vector for transmission (Leidenberger et al., 2007), as one study found larval stages of filarioids in seal lice (Geraci et al., 1981). *A. spirocauda* and the blood sucking ectoparasite *Echinophthirius horridus* were highly prevalent in yearling harbour seals, supporting the hypothesis that seal lice may act as vectors for heartworms in seals (Lehnert et al., 2015). The seal louse *E. horridus* is transmitted directly during physical contact between harbour seals e.g. at haul-out sites and during social interactions such as pup nursing and reproduction (Geraci et al., 1981). Seal lice can cause dermatitis and anaemia in severe infections, but prevalence is relatively low (~4%) and severe infections are rarely encountered (Lehnert et al., 2015).

3.1.5. Respiratory mites

The endoparasitic mite *Halarachne halichoeri* causes different levels of upper respiratory disease in both harbour seals and grey seals (Fig. 12). Historical reports of *H. halarachne* in the German Baltic Sea date back to the end of the 19th century (Nehring, 1895, 1884; Reckendorf et al., 2019). However, with the disappearance of the grey seal because of human over-exploitation (Olsen et al., 2018) during the 19th century (Reijnders et al., 1995), this mite was not reported for more than a century. A recent study reports the first and subsequent

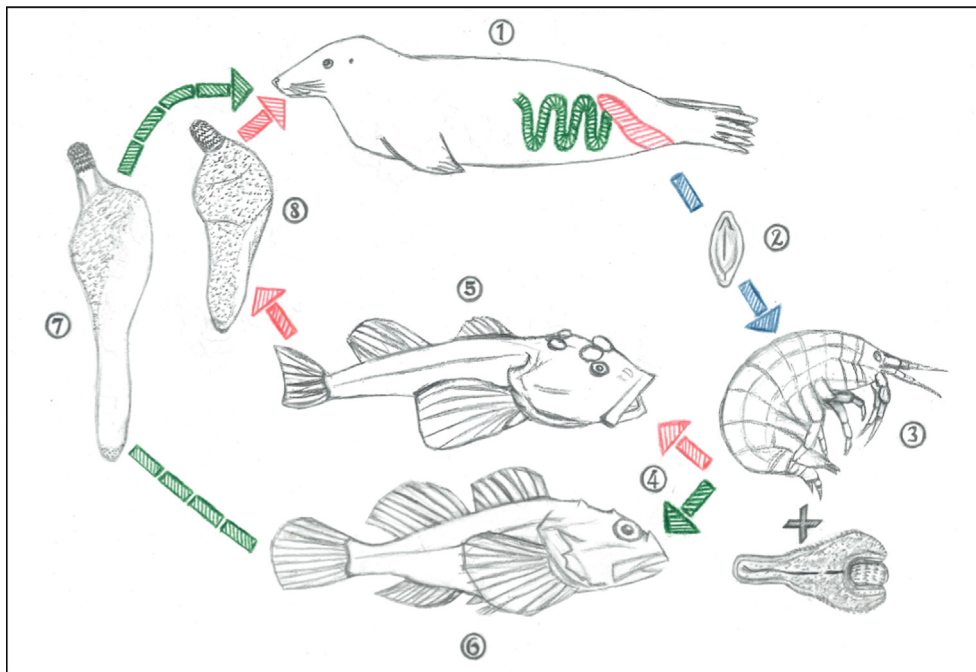


Fig. 11. Life cycle of *Corynosoma strumosum/semerme*. 1: grey seal final host, infected small intestine (green)/colon (red); 2: eggs shed with faeces; 3: amphipod intermediate host (*Monoporeia affinis*) ingests acanthocephalan eggs -> development of acanthocephalan larval stages: acanthor -> acanthella -> cystacanth in amphipod; 4: cystacanth ingested by paratenic fish hosts; 5: fourhorn sculpin (*Myoxocephalus quadricornis*) and 6: shorthorn sculpin (*Myoxocephalus scorpius*); 7: *C. strumosum* transmitted by shorthorn sculpin (*M. scorpius*); 8: *C. semerme* transmitted by fourhorn sculpin (*Myoxocephalus quadricornis*) to grey seal final host via infected fish, cystacanth matures in final hosts intestine, *C. strumosum* infects seal small intestines, *C. semerme* seal colons.

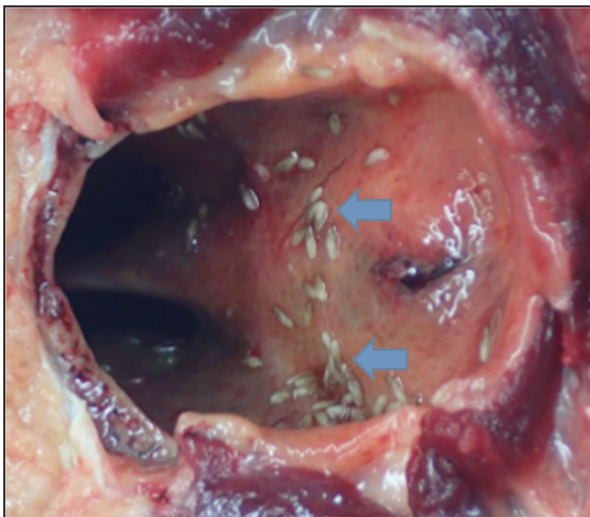


Fig. 12. Severe *Halarachne halichoeri* infection in the nasal cavity (arrows) of a grey seal.

findings of *H. halichoeri* in grey and harbour seals of the North and Baltic Seas in 2014 and onwards (Reckendorf et al., 2019). As such, the re-emergence of this endoparasitic mite in North Sea and Baltic habitats seems to have occurred simultaneously with the recolonisation of its primary host, the grey seal, since the 1980s (Harding and Härkönen, 1999). During the course of recolonisation, it was likely transmitted to harbour seals at shared haul-out sites.

3.1.6. Protozoan parasites

Marine mammals are susceptible to infection with the zoonotic protozoan parasites *Giardia*, *Cryptosporidium* and *Toxoplasma* (Cabezón et al., 2011; Fayer et al., 2004; Herder et al., 2015; Reboredo-Fernández et al., 2015) and are increasingly exposed to these pathogens due to run-off, farming and anthropogenic impacts in coastal areas (Fayer et al., 2004; VanWormer et al., 2016). While it is known that *Toxoplasma* can cause fatal infections in harbour porpoises and seals (Herder et al., 2015; van Pelt and Dieterich, 1973), the health-consequence to marine mammals of harbouring protozoans such as

Cryptosporidium and *Giardia* is largely unknown.

A study surveying protozoan infections in North Sea and Baltic marine mammals (Grilo et al., 2018) investigated fecal samples from harbour seals ($n = 68$), harbour porpoises ($n = 15$) and grey seals ($n = 8$), using a modified Ziehl-Neelsen technique. Low prevalence (2 and 0%) were detected for *Cryptosporidium* spp. and *Giardia* spp., respectively, in seals from the North Sea. Of the 15 Baltic harbour porpoises, 12 showed no signs of infection with either protozoan. This pilot study thereby indicates to a low occurrence of *Giardia* and *Cryptosporidium* in Baltic marine mammals. H

However, molecular techniques and a bigger cohort needs to be investigated to further elucidate the situation. Arctic ringed seals, as well as harp- (*Pagophilus groenlandicus*), hooded- (*Cystophora cristata*) and bearded seals (*Erignathus barbatus*), are known to be infected with *Cryptosporidium* spp. and *Giardia duodenalis*, including zoonotic *Giardia* strains (Appelbee et al., 2010; Dixon et al., 2008), suggesting that Baltic seal species may also be exposed to infection.

3.2. Birds

A single study has reported on parasites in Baltic eiders (Garbus et al., 2018). The authors collected dead birds during two spring time mortality events in 2007 and 2015 from Christiansø, Denmark. Necropsies showed a body weight around 50% of normal and severe infections with the acanthocephalan parasite *Polymorphus minutus*. Evaluation of gross morphology could not identify any other causes of mortality. The findings were likely due to suboptimal feeding conditions which, in combination with a high parasitic burden, caused high physiological/energetic stress and mortality. Associated ecosystem dynamics and factors have yet to be identified, however, factors such as slower growth of blue mussels (*Mytilus edulis*), invasive mussel species and toxic algae blooms linked to a warmer climate have been proposed (Larsson et al., 2014; Laursen and Møller, 2014).

4. Viruses

4.1. Marine mammals

4.1.1. Morbillivirus

The Morbillivirus genus consists of a group of highly infectious,

enveloped non-segmented, negative strand RNA viruses belonging to the *Paramyxoviridae* family (Nambulli et al., 2016). To date seven viruses are recognized as species of the Morbillivirus genus, of which Phocine Distemper Virus (PDV), Canine Distemper Virus (CDV) and Cetacean morbillivirus (CeMV) are known to infect and cause mortalities in marine mammals (Härkönen et al., 2006; Jo et al., 2018). CDV infects a broad range of terrestrial and marine carnivore species, including the Baikal seal (*Pusa sibirica*) and the Caspian seal (*Pusa caspica*), but has not yet been reported in Baltic seals. In contrast, PDV has been a major pathogen to harbour seals in the Baltic region. Infected animals suffer from fever, coughing, dyspnoea, oculo-nasal discharge, conjunctivitis, ophthalmitis, keratitis, diarrhoea, increased buoyancy caused by emphysema, disturbances in the central nervous system and potential abortion. The main pathological findings in infected seals are secondary bacterial pneumonia with emphysema and oedema (Bergman et al., 1990; Jauniaux et al., 2001; Kennedy, 1998).

PDV was first described in 1988 when a mass mortality event caused the death of approximately 23,000 harbour seals in northern Europe, and in 2002, a second PDV outbreak occurred killing around 30,000 harbour seals (Härkönen et al., 2006). The virus is also causing mortalities in Northwest Atlantic harbour seal populations, and PDV antibodies have been found in several Arctic seal species, indicating that PDV is endemic to the Arctic. It has been suggested that the virus causing the 1988 epizootic was introduced to European seals by migrating harp seals, whereas the 2002 outbreak seems to be a result of a single introduction by an unknown carrier (Dietz et al., 1989; Härkönen et al., 2006; Kreutzer et al., 2008; Stokholm et al., 2019). While causing high mortality in harbour seals, the outbreaks only resulted in low mortality in sympatric grey seals which were suggested to act as carriers of the virus (Bergman et al., 1990; Härkönen et al., 2006). Notably, the initial cases of both outbreaks were found in the spring at Anholt island in the Danish part of the Kattegat from where it, spread to the adjacent harbour seal colonies (Härkönen et al., 2006), possibly through series of independent transmission events (Stokholm et al., 2019). Further support for the harp seal facilitated introduction in 1988 was obtained when an additional virus subtype was found in the data set suggesting that at least two introductions occurred (Stokholm et al., 2019).

4.1.2. Influenza A virus

Influenza A virus is a highly infectious zoonotic pathogen found in birds and mammals, which is able to adapt, mutate and hybridise during intra- and interspecific transmissions and co-infections. Although typically a pathogen of water fowl, the virus has been detected across a range of marine mammal species, including harbour seal, minke whale (*Balaenoptera acutorostrata*) (Lvov et al., 1978), long-finned pilot whale (*Globicephala melas*) (Hinshaw et al., 1986) and northern elephant seal (*Mirounga angustirostris*) (Fereidouni et al., 2014; Goldstein et al., 2013).

Influenza A has caused multiple unusual mortality events among harbour seals in the north-western Atlantic (Puryear et al., 2016), but was first detected in European harbour seals in 2014, when seals in Denmark, Sweden, Germany and the Netherlands were infected by a highly pathogenic influenza A strain (H10N7) that caused the death of several thousand animals (Bodewes et al., 2015; Krog et al., 2015; Zohari et al., 2014). The pathological findings included severe pneumonia with congestion, moderate to high amounts of blood in the thorax ('hemothorax'), intensely hyperaemic trachea and blood in/from the mouth (potentially from 'hemoptysis', i.e. coughing up blood). Secondary bacterial infections of the lungs by e.g. *Pseudomonas aeruginosa* and *Streptococcus equi* ssp. *zooepidemicus* were identified – both of which are zoonotic. Genetic analysis of virus isolates from a large number of animals (Bodewes et al., 2016; Siebert et al., 2017) found that the mutation rate was higher at the beginning, than at the end, of the outbreak. This suggests that the virus initially underwent a series of adaptations in order to transmit from bird to mammal and thereafter

efficiently spread among the harbour seal population.

4.2. Birds

4.2.1. Infectious bursal disease virus

Eiders are also susceptible to infectious bursal disease virus (IBDV). A seroprevalence of up to 96% was detected in the Baltic Sea by e.g. Söderskär, but no pathology was associated with this (Hollmén et al., 2000). It is therefore unknown if this virus causes immune suppression in the Baltic eiders.

4.2.2. Influenza A virus

A single study has reported influenza A in Baltic sea eagles (Krone et al., 2018). The virus killed at least 17 eagles in Northern Germany during the winter 2016–17. The eagles were young individuals, and pathological investigations showed necrotising encephalitis. Another study investigated the seroprevalence of influenza A in 319 pink-footed geese with a flyway across the Baltic Sea when migrating from the Netherlands and Denmark towards Norway and Finland (Hoye et al., 2011). The study showed that ca. 60% of adults had influenza antibodies, while only 15% of the young birds had antibodies against influenza. The prevalence was highest in spring and lowest in late summer, suggesting that different ecological niches and ecosystems affect the disease dynamics of this species. In another study by Lam et al. (2020), the prevalence of eiders in the Western Baltic showed a sero-prevalence of 55% in eiders samples 2016–2018 (n = 183).

5. Bacteria

5.1. Marine mammals

Little is known about the occurrence of pathogenic bacteria in Baltic marine mammals. In one study of post-mortem findings in harbour porpoises in the North and Baltic Seas, isolated bacteria considered potentially pathogenic included *Aeromonas* spp., *Bacteroides fragilis*, *Clostridium perfringens*, *Erysipelothrix rhusiopathiae*, *Escherichia coli* var. *haemolytica*, *Klebsiella* spp., *P. aeruginosa*, *Salmonella* spp., *Serratia* spp., *Staphylococcus aureus*, *Staphylococcus intermedius*, α - and β -haemolytic streptococci and *Vibrio anguillarum* (Siebert et al., 2001). Here, α - and β -haemolytic streptococci were consistently found to be associated with bronchopneumonia, as well as with parasitic infection and abscessation. *S. aureus* and β -haemolytic streptococci were identified in association with myocarditis, pyelonephritis and septicemia in neonates and calves (Siebert et al., 2001). Furthermore, α -haemolytic streptococci, *E. rhusiopathiae* and *E. coli* var. *haemolytica* were isolated from blood and organs and, as such were associated with septicemia (Siebert et al., 2001).

Another study looked broadly into differences in the bacterial flora of harbour porpoises in the North Sea, the Baltic Sea and Norwegian, Greenlandic and Icelandic waters through a broad multi-organ screening for pathogenic bacteria using classical microbiological analyses (Siebert et al., 2009). In regions characterised by relatively few anthropogenic impacts, only a few pathological bacteria could be isolated from harbour porpoises. In contrast, harbour porpoises in the highly impacted North and Baltic Seas contained isolates of potentially pathogenic bacteria including *Brucella* spp., *C. perfringens*, *E. coli*, *E. rhusiopathiae*, β -haemolytic streptococci and *S. aureus*. The most abundant bacteria were α -haemolytic streptococci, *Pseudomonas* spp. - including *P. aeruginosa* - and *E. coli* including *E. coli* var. *haemolytica* and *Escherichia adecarboxylata*. In all regions, the main pathological finding associated with bacterial growth was bronchopneumonia followed by – at least in the North and Baltic Seas – hepatitis, enteritis and lymphadenitis. Across regions, the bacteria most frequently associated with pathological findings were *E. coli* - including *E. coli* var. *haemolytica* - and β -haemolytic streptococci, whereas *S. aureus* was more frequently isolated in the Baltic Sea than in the North Sea (Siebert et al., 2009). An

association of *S. aureus* septicaemia with pyogranulomatous myocarditis, necrotising suppurative bronchopneumonia, pyelonephritis, osteomyelitis and leptomeningitis was reported for two harbour porpoises from the German and Danish Baltic Seas, respectively (Siebert et al., 2002).

Finally, a study on the isolation and molecular characterisation of β -haemolytic streptococci reported *Streptococcus dysgalactiae* ssp. *dysgalactiae* from lung and kidney tissue in two harbour porpoises from the Baltic Sea (Siebert et al., 2017; Swenshon et al., 1998), and another study isolated *Streptococcus phocae* from two Baltic grey seals (Siebert et al., 2017; Vossen et al., 2004).

Bergman (2007) reported that β -haemolytic streptococci were the most common bacteria found in grey, ringed and harbour seals investigated between 1997 and 2002. β -haemolytic streptococci were found in lesions affecting the respiratory tract, uterus, colon as well as in a few cases of bacteraemia and septicaemia. In two cases of septicaemia, *Aeromonas hydrophila* was found. Krovacek et al. (1998) also reported one of these cases, implying that a large skin wound could be the possible point of entry. Bergman (2007) also found other bacteria, e.g. *E. coli*, and *Pasteurella* spp., in various tissues.

5.2. Birds

Aviary cholera caused by *Pasteurella multocida* has been reported in Baltic eiders over the past decades (Laursen and Møller, 2014). A colony study at Helleholm analysed adult survival of females in the period 1998–2012. The authors showed a rather constant survival similar to that of other studies, while years with low adult survival were associated with outbreaks of avian cholera (Tjørnløv et al., 2013). This suggests that avian cholera, at least in this colony, is more important for adult survival than, is for example winter temperature. Altogether, this may partly explain the population dynamics and fluctuations of Baltic eiders over the past decades and suggests that food web changes and dynamics associated with, for example, climate are important for the conservation of these populations (Laursen and Møller, 2014).

6. Disease susceptibility and immunity

A competent immune system plays an important role in protecting animals from infections. Thus, immunocompromised individuals are more susceptible to disease. The abundance and variety of bacteria in the environment increases with the proximity to discharge of human sewage into near shore waters (Haebler and Moeller Jr, 1993). Consequently, animals living in areas with high anthropogenic influence are supposedly more affected by bacterial infections than are animals in more remote regions. In line with this, two studies reported bacterial pneumonia and septicaemia to be among the most common causes of death in marine mammals of the North and Baltic Seas (Siebert et al., 2001; Wunschmann et al., 2001).

The underlying patterns of influenza and morbillivirus susceptibility and immunity are poorly described for marine mammals. Low mortality and prevalence of morbillivirus antibodies among harbour seals above the age of 14 during the 2002 outbreak suggest that the animals surviving the 1988 outbreak had developed some degree of immunity (Bodewes et al., 2013; Härkönen et al., 2006; Ludes-Wehrmeister et al., 2016). In a serological screening of 29 harbour seals sampled in 1992 and 1996–1998, all animals had antibodies against either CDV or PDV, but in 2010 and 2014, only 9% and 2% of the seals had antibodies, respectively. Currently this number is approaching 0% (Bodewes et al., 2013; Ludes-Wehrmeister et al., 2016). The decreasing seroprevalence, along with growing populations of both harbour and grey seals, imply a high risk of future infection and potential high mortality. Another factor that may potentiate risk of infection is high concurrent contaminant loads of the host which may reduce the function of the immune system. This is leading to increased infection rates and mortalities through decreased lymphocyte viability among others (Desforges et al.,

2016). Feeding experiments of seals with fish from polluted marine regions in the 1990s revealed a higher susceptibility to virus infections (de Swart et al., 1996; Ross et al., 1996), and *in vitro* studies suggest increased viral replication of PDV in harbour seal immune cells exposed to PCB (Bogomolni et al., 2016). But, in contrast, *in vitro* exposure to organochlorinated contaminants (OCs) was found to reduce influenza A virus infectivity in Madin Darby Canine Kidney (MDCK) cells and human lung epithelial cells, implying that the underlying host-pathogen-pollutant interactions are complex (Desforges et al., 2018).

Baltic mammals and birds are exposed to a broad spectrum of pathogens. In terms of bacteria, testing has thus far mainly relied on classical bacteriology, including selective or non-selective growth media, isolation and classical identification. Classical bacteriology presents weaknesses in terms of the identification of unknown bacteria or of bacteria that are hard to cultivate using standard growth media and physical conditions. Screening for pathogens using antibodies typically reflects past, rather than ongoing, infections and may not offer sufficient detail on the type or strain. PCR-based assays and the development of high throughput sequencing offer higher sensitivity for detecting unknown pathogens and do not rely on live pathogens. The cost and efficiency of genetic sequencing methods have improved considerably during the last 10 years, and they offer an analytical potential in the study of significant pathogens. Particularly, parasites like *C. semerme* in the colon and the emerging *P. truncatum* in the livers of Baltic grey seals need to be monitored as well as anisakid nematodes due to their health effect on the animals. In addition, distribution of viral and bacterial pathogens as well as emergence and spread of new pathogens need to be monitored to assess the health status of key species in the Baltic Sea. This is of special importance as some of the occurring pathogens are zoonotic, thus also posing a potential risk for humans. Marine mammal handlers, as well as civilians that by chance encounter marine mammals, need to be aware of this risk. It is important to continue the monitoring of diseases affecting the Baltic key species to assess the relation to population dynamics as well as disease threat to humans.

7. Conclusions

Overall, Baltic high trophic key species are exposed to multiple infectious agents that may affect their population level. There are reports of parasites and bacteria infections secondary to PDV and Influenza A outbreaks and recent prevalence of seal parasites that should be continued monitored. White-tailed eagle, common eider and pink-footed geese showed fewer outbreaks of mortalities due to infectious agents when compared to seals. The emergence and spread of new pathogens should be screened for of key Baltic species. This is of importance as the occurring pathogens may be zoonotic and thus pose a potential risk for humans including marine mammal handlers, as well as civilians. Infectious agents are valuable indicators of host ecology and can act as bioindicators of the distribution, migration, population dynamics, diet and behaviour of marine mammals and birds. These diseases affect the health of the entire ecosystem, and consequently ecosystem function and services, and as global warming is continuously increasing, the impact of global change on infectious disease patterns is important to monitor in Baltic key species in the future.

Declaration of Competing Interest

None of the authors of this paper have a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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Appendix A. Supplementary data

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